

lines lying on a cubic surface. This theorem may be deduced from the equation

$$xyzv = (x + aT)(y + bT)(z + cT)(u + dT),$$

where  $T = \alpha x + \beta y + \gamma z + \delta u$ ; and  $a, b, c, d, \alpha, \beta, \gamma, \delta$  are constants. The equations of twelve lines on the surface are evident.

This paper shows how the remaining fifteen straight lines on the surface may be obtained by means of nothing higher than quadratic equations, and determines which of these lines intersect each other.

The paper then proceeds to give a graphical method of representing all the intersections of the twenty-seven lines on a cubic surface by means of a plane diagram, which admits of many interesting transformations.

By the help of such diagrams some of the known relations of the twenty-seven lines to each other are deduced, and some theorems with respect to the lines, which it is believed are new, are established; for instance, the number of closed quadrilaterals, pentagons, and hexagons on the surface is determined, as well as the number of ways in which nine triple tangent planes can be drawn to pass through all the twenty-seven lines, and the number of ways in which twelve of the lines can be chosen, so that they are the intersection of two tetrahedrons in perspective.

## XII. "Further Observations on the Shoulder Girdle and Clavicular Arch in the Ichthyosauria and Sauropterygia." By H. G. SEELEY, F.R.S. Received May 25, 1893.

On January 18, 1892, I communicated to the Royal Society observations on the nature of the shoulder girdle and clavicular arch in Sauropterygia, which were read on February 18, and published in the Proceedings on June 25, 1892. These studies had grown out of the examination of new remains of Anomodont Reptiles, which I obtained in South Africa; and were the result of an endeavour to gain a knowledge of structures in which the shoulder girdle in extinct Reptilia admitted of detailed comparison with those materials. I had made examination of the same region of the skeleton in Plesiosaurs and Ichthyosaurs, and communicated the results to the Geological Society, which were published in the Journal of that Society in November and December, 1874.

In the paper of 1892 I endeavoured to correct, enlarge, or justify interpretations previously given. One aspect of this revision led to a controversial paper, challenging some points of interpretation which occur among the facts in my contribution. It is entitled "On the Shoulder Girdle in Ichthyosauria and Sauropterygia," by J. W. Hulke,

F.R.S., received by the Royal Society April 11, read May 12, 1892. All that was then before the Fellows is printed in the Proceedings for August 26, 1892, p. 471, and the paper was printed in No. 316 of the Proceedings. As my own paper had not been published when that by Mr. Hulke was read, and as his paper is entirely devoted to controverting my conclusions and discrediting the existence of evidence which is there figured, it is obviously based upon an imperfect knowledge of the facts. I should have been content to have left the vindication of the truths and ideas which I endeavoured to state to others, but that I had no opportunity of meeting the author's contentions, when the abstract of his paper was read; and because there are misconceptions of my meaning, some of which I should be glad to remove. The point of view taken by Mr. Hulke as the foundation for his criticisms is said to be mainly embryological work upon existing Reptiles and Amphibians, the exact relation of which to the extinct Ichthyosauria and Sauropterygia cannot be stated with precision, though all writers concede that the groups compared, Urodela, Anura, Lacertilia, are distinct orders; and I believe that the differences between them are too great to be expressed in this way. The embryology of Ichthyosaurs and Plesiosaurs being necessarily unknown, it seems to me that no sound interpretation of the obscure parts of their skeletons can be based upon such evidence; unless it is previously shown that there is a predominant affinity of the extinct organic type with the recent type to which it is compared. I should, therefore, attach less value than does Mr. Hulke to the embryological considerations which he adduces in relation to the identification of bones as being omosternal on the one hand, or clavicular on the other, and as determining the existence or absence of a precoracoid element in these extinct animals. Rather than import into discussion such hypothetical foundations for nomenclature of the bones of the skeleton in extinct animals, I prefer to trust to visible evidence of the relative position of the disputed bones, and to such comparisons with their condition in allied animals as may appear to justify inferences as to their true nature.

In discussing the shoulder girdle in Ichthyosauria, I have suggested that the conditions of the bones appear to indicate a precoracoid element, which was cartilaginous, and was not preserved. I assume that such an element may have extended from the scapula to the coracoid, transversely in front of the coracoid, and anteriorly between it and the clavicle. To this suggestion Mr. Hulke replies that the appearance of a division of the articular end of the scapula into three parts is fallacious (*loc. cit.*, p. 234) and illusory (p. 235). The basis for this statement is said to be a careful study of many Ichthyosaurian scapulæ, and especially of a separate scapula lent by Mr. A. N. Leeds, F.G.S. Mr. Hulke finds that the Oxford Clay scapula com-

prises in this region only two parts—"one posterior, glenoid, diarthrodial segment; the other, an anterior synchondrosial segment, which articulated with the coracoid." This is a point upon which I may state that in describing *Ophthalmosaurus*\* I suggested the view which Mr. Hulke has adopted. But I appeal from those disconnected bones to the evidence from the specimens in museums like the national collection. The Natural History Museum contains isolated scapulæ, but it also contains some scapulæ in natural position in the skeletons from the Lias, and there are other skeletons exhibiting the shoulder girdle in good preservation in the Geological Museum at Cambridge and elsewhere.

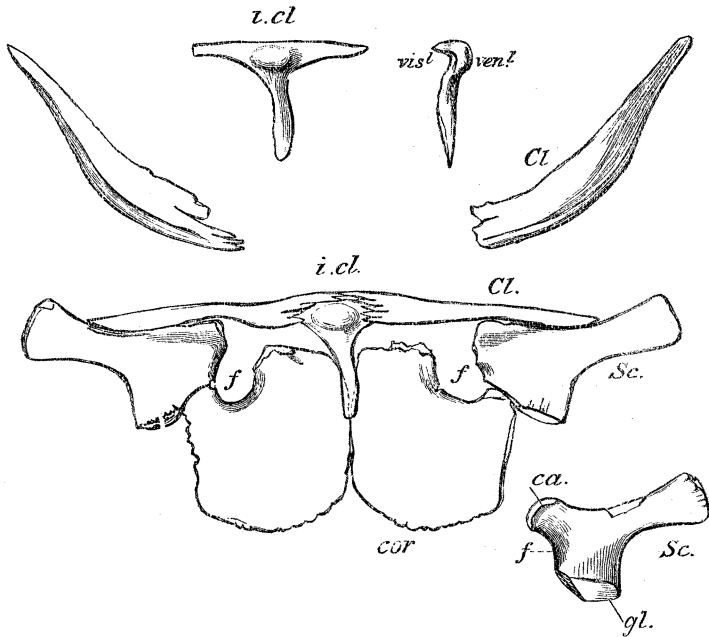


FIG. 1.—Shoulder girdle of *Ophthalmosaurus*. *i.cl.*, front aspect of interclavicle; on the right is a side view of this bone, showing its ventral and visceral contours. Beneath it are the posterior surfaces of the right and left clavicles (*Cl.*). Below this all the bones of the shoulder girdle are put together. The interclavicle is embraced by the clavicles; and (*cor.*) coracoid and scapula (*Sc.*) contribute to enclose the coracoid foramen (*f*). On the right and lower corner is an isolated scapula, with the margin of the coracoid foramen (*f*) completely ossified, preserving the cartilaginous surface (*ca.*). *gl.*, humeral articulation.

\* 'Quart. Jour. Geol. Soc.,' 1874, vol. 30, pp. 693, 703. Pl. XLV, fig. 1, is a left coracoid. The surface lettered *c* is the humeral articulation; the surface *s* is the intercoracoid suture.

When the bones occur separate the scapula can usually be fitted to the coracoid; then the surface which formed part of the articulation for the humerus is clearly distinguishable from the surface which joined the coracoid. And if the antero-posterior extent, or measurement from within outward, of the coracoid surface which articulated with the scapula is taken, it will be found to be greatly exceeded by the length of the opposed surface of the scapula, as it extends from the humeral articulation forward to the clavicle. So that there is a free edge of the scapula, which is cartilaginous, extending in front of its coracoid articulation, and between that articulation and the clavicle. This surface is distinct from the coracoid surface, first in being much thinner; and, secondly, in commonly making an angle with that surface, though I do not attach much importance to the latter circumstance, as it may be affected by conditions of preservation and completeness of ossification. In one species of *Ophthalmosaurus*, in the British Museum, a part of this margin of the scapula anterior to the coracoid is concave and completely ossified where it formed part of the coracoid foramen (fig. 1, lower right-hand figure), but anterior to that is the unossified surface, which I suppose to have been for the precoracoid cartilage. On the inner anterior margin of the coracoid will also be found a surface, which indicates a cartilage, which I believe met the clavicle. The examination of the skeleton shows that the tripartite division of the scapula at its articular end, as figured by Cuvier, and as represented by Sir E. Home, to whom the sternal bones were first pointed out in detail by Buckland, as drawn by De la Beche for Sir E. Home, as represented in Professor Huxley's figure, and as affirmed by myself, cannot be regarded as illusory or fallacious on the evidence given; and at present no reference has been made to any skeleton from which such an inference could be drawn, or even in which the different condition affirmed by Mr. Hulke could be seen, though there is no reason why such a condition should not be found.

The importance of this discussion centres round the significance of the notch or concavity on the anterior border of the coracoid, which is placed towards the scapular margin. Does that notch represent the coracoid foramen of existing Reptiles? Such a foramen is seen in the coracoid bone in Lizards and *Hatteria*, and has been regarded as marking the union of the precoracoid and coracoid elements into one bone, and on that account I have spoken of it as the precoracoid foramen. It is more distinct in Amphibians, though it is differently placed. It occurs in Crocodiles. Among extinct animals it is found in the Saurischia and Ornithischia. It is present in the scapular arch of *Pareiasaurus* and Anomodonts. It may be compared to the foramen in *Ornithorhynchus* between the scapula and precoracoid. If the notch in the coracoid of *Ichthyosaurus*, which is towards the scapula, should be regarded as representing the coracoid foramen of any of

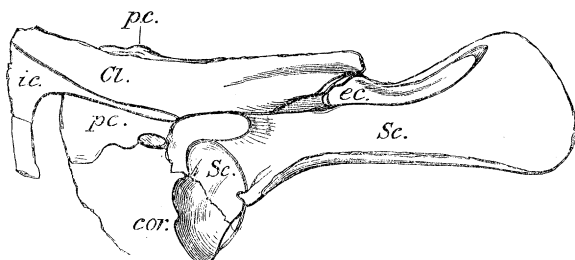


FIG. 2.—Left shoulder girdle of *Pareiasaurus Baini* as the bones were found before the matrix had been removed to separate the clavicular arch from the scapular arch. *ic.*, interclavicle; *Cl.*, clavicle; *pc.*, precoracoid; *cor.*, coracoid; *Sc.*, scapula; *ec.*, epiclavicle.

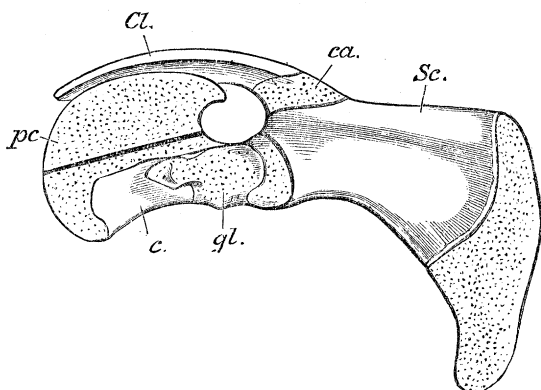


FIG. 3.—Shoulder girdle of a young *Ornithorhyncus*, after G. B. Howes, reduced and reversed. The dotted parts (*Ca.*) are cartilage; *Cl.*, clavicle; *pc.*, precoracoid; *c.*, coracoid; *Sc.*, scapula; *gl.*, humeral articulation.

these groups of animals, living or extinct, then it would, from the analogy of shoulder girdles which from age or plan are imperfectly ossified, be a legitimate inference, I submit, that the foramen which was defined on the one side by bone was completed on the other side by cartilage. The notch is in such a position that it is comparable to a coracoid foramen. No other determination for it has been suggested. If this identification were admitted, it seems to me highly probable, from comparison of the scapular arches in extinct Sauromorpha, that the cartilage which extended inward from the scapula was continuous with the cartilage which extended forward from the coracoid, and that the intermediate part defined the anterior margin of the foramen. If I understand Mr. Hulke, he would admit the existence of such a cartilage as an inference supported by analogy ;

for he states, "the recess between the truncated antero-external corner of the coracoid and the adjacent antero-inferior angle of the scapula, both which parts bear, as Professor H. G. Seeley says, the mark of having had cartilage attached to them, is just the situation where a wider band of synchondrosial cartilage might be expected than was present posteriorly where the scapula and coracoid were nearer together. This passage seems to me practically to admit the point which I have affirmed, that the scapula shows a third cartilaginous attachment in addition to the two surfaces giving attachment to the coracoid and the humerus. Secondly, I urged that this cartilage probably connected the scapula with the inner truncated anterior border of the coracoid. No evidence is offered against this conception.

Then the only question of importance is by what name such a cartilage might be known. Mr. Hulke regards it as a persistent remnant of the *continuum* in which the bones originated. I prefer to name it precoracoid, because if it were a primitive cartilage which did not belong to either bone, it might be expected to be encroached upon by scapula or coracoid, or both; but during the whole period of time in which the genus *Ichthyosaurus* is found, there is no conclusive evidence of any such extension of ossification upon the scapula or coracoid. Neither scapula nor coracoid alter their forms at the expense of the supposed cartilaginous *continuum*; and, therefore, I infer that the cartilage was not ossified, but persisted as a precoracoid, though, as the coracoid foramen enlarged, the amount of cartilage left to represent it might become small. If the foramen enlarged so as to divide the cartilage into inner and outer portions, the external part adjacent to the scapula and coracoid would still be precoracoid, though the part adjacent to the inner anterior edge of the coracoid might assume the aspect of an epicoracoid. Such a separate condition of cartilages I understand Mr. Hulke to admit.

In my discussion of the shoulder girdle (*loc. cit.*, p. 120) it is remarked that I have failed to find "a specimen which leads me to doubt the substantial accuracy of the early interpretations of Home, Buckland, and Cuvier, in regarding the scapula as extending an articular surface inward and forward towards the pre-articular portion of the coracoid." This passage is referred to by Mr. Hulke in the following words: "In support of his conception of a precoracoid—cartilaginous—in Ichthyosauria, Professor H. G. Seeley cites the opinion held by Sir E. Home, Buckland, and Cuvier respecting the position and relations of the scapula." The two statements are not identical. Mr. Hulke reproduces the first of Sir E. Home's figures (p. 237) of the shoulder girdle, which I have known as "the Buckland figure," to distinguish it from the "De la Beche figure," given in the 'Phil. Trans.,' 1819, Pl. 14.

Home's first figure is spoken of as showing "unnatural proportions of the several bones." It is a generalised figure in which the scapulæ and the clavicles which rest upon them are about one-third too long, and the interclavicle is about twice as wide in the staff as any specimen which I remember (though, perhaps, not wider than in a specimen figured by Cuvier), but in substantial accuracy of arrangement of the bones the figure is admirable, and would be marvellous if made, as Mr. Hulke implies, from dissociated bones. Mr. Hulke does not point out any inaccuracy in the figure, which he reproduces, and no evidence is referred to which is opposed to the position of the scapula indicated in Pl. 2, fig. 1, 'Phil. Trans.,' 1818.

In the same way the criticism upon Cuvier seems to me without justification. It is stated by Mr. Hulke that, since "Cuvier copies both the figure given by Sir E. Home and the figure given by Dean Conybeare, and abstains from expressing his own views on the subject (of the difference between them), obviously little weight attaches to his authority in regard to it."

In the first place, Conybeare and Home agree in representing an anterior surface of the scapula in advance of the articulation of that bone with the coracoid. Secondly, Cuvier, in the plate in which Home's figure is copied, gives several admirable engravings of the shoulder girdle from specimens, and his fig. 1 and fig. 5 demonstrate that the scapula did extend a cartilaginous surface in advance of the articulation with the coracoid. A cast of the specimen represented in fig. 5 is preserved in the Natural History Museum. Cuvier's figures show variations in size of the anterior notch between the coracoid and scapula.

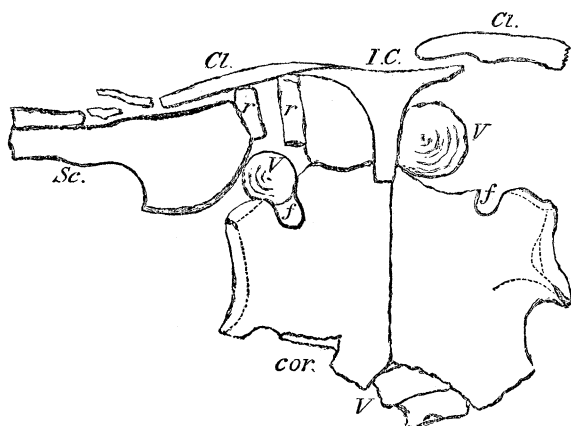


FIG. 4.—Shoulder girdle of *Ichthyosaurus*, after Cuvier,  $\frac{1}{3}$  natural size ('Oss. Foss.,' Pl. 258, fig. 1). *I.C.*, interclavicle; *Cl.*, clavicle; *cor.*, coracoid; *Sc.*, scapula; *f*, coracoid foramen; *V*, vertebrae; *r*, ribs.

In fig. 4 it approaches nearer to the form of a foramen perhaps than in any other specimen, and in the interspace between the truncated anterior margin of the coracoid and the clavicle a surface is left smooth and distinct from the matrix in Laurillard's drawing, which may be only a hole in the matrix,\* but that appearance possibly may be the foundation for the supposed epicoracoid described by the late Sir R. Owen in 1839 and 1866.

I fail to find any support for the critical position taken by Mr. Hulke, or for his restoration of the shoulder girdle of *Ichthyosaurus* ('Geol. Soc. Quart. Jour.,' 1883, p. 45), in the criticism which he makes of the authors referred to, who all take the view of anterior extension of the scapula in advance of the coracoid articulation;

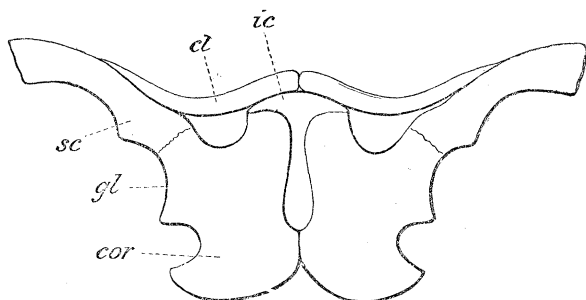


FIG. 5.—Mr. Hulke's restoration of the Ichthyosaurian shoulder girdle. *ic*, interclavicle; *cl*, clavicle; *sc*, scapula; *cor*, coracoid; *gl*, articulation for humerus.

while in Mr. Hulke's figure the breadth of the articular end of the scapula is made the same as the breadth of the surface of the coracoid with which it unites. This is at variance with every specimen known to me. The difference between Mr. Hulke, on the one hand, and other writers is not a matter of opinion or interpretation, but of fact, which can only be demonstrated by examination of specimens, or figures in detail of the structure, shown in all specimens which I have seen in skeletons well preserved.

I have stated that this identification of the precoracoid accounts for the structure of the shoulder girdle, and explains its homology. As both clauses of this statement are challenged, I may state, further, that by "structure" I mean the mode of arrangement of the bones by which the cartilaginous surface of the scapula extends forward in advance of

\* Professor Albert Gaudry has had the kindness to examine this specimen for me, and has had the matrix partly removed so as to make the relations of the scapula and coracoid more evident. He finds no trace either of ossification or cartilage between the coracoid and clavicle.



the coracoid; and by "homology" I mean that, since the coracoid foramen is not in the middle of the coracoid bone, the Ichthyosaurian coracoid is not homologous with the Lacertilian coracoid; and, since this foramen in *Ichthyosaurus* is not defined by the coracoid and scapula, but could only be completed by a structure which occupied the open angle between the coracoid and scapula, the coracoid is not homologous with that of Saurischia or Ornithischia; and can only be compared with the coracoid of an animal in which a separate precoracoid is developed. I had not realised that this was a conclusion on which comparative anatomists have been in accord.

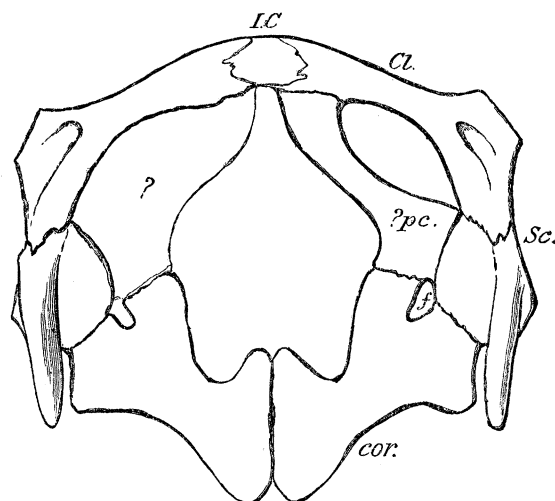


FIG. 6.—Shoulder girdle of *Nothosaurus mirabilis* restored. *I.C.*, interclavicle; *Cl.*, clavicle; *Sc.*, scapula; *cor.*, coracoid; *f.*, coracoid foramen; *?pc.*, hypothetical cartilaginous precoracoid. On the left side this element (?) is represented as possibly extending along the clavicle, as in *Ornithorhynchus* and *Ichthyosaurus*.

I have also advocated the identification of the precoracoid as bringing the shoulder girdle of *Ichthyosaurus* into harmony with that of *Nothosaurus*, because in that genus there is a similarly incomplete coracoid foramen, and similar internal cartilaginous surfaces truncating the coracoid anteriorly and the scapula internally so as to include an angle between them, which such a cartilaginous precoracoid would occupy, so as to complete what I regard as the coracoid foramen. I only know the Nothosaurian shoulder girdle from von Meyer's excellent figures, and in contesting my interpretation I do not gather that Mr. Hulke has better knowledge of the original materials. It is urged that I am in error in identifying the coracoid foramen of

*Nothosaurus* with that of *Ichthyosaurus*. I have not proposed to identify it with the coracoid foramen in the coracoid of a Lizard, because I believe with Mr. Hulke that the precoracoid in Lizards is ossified. And it is because I find no evidence that the precoracoid is ossified in *Nothosaurus* (and I do not think there should be any contention that it is ossified, now that Mr. Hulke accepts the existence of clavicles in that genus) that I cannot regard the Lacertilian coracoid as homologous with the Nothosaurian coracoid. It is suggested by Mr. Hulke that the "coracoid foramen" in the Nothosaurian coracoid is not to be found in the small open notch which faces towards the scapula (*f*, fig. 6), but in the deep depression in the anterior contour of the coracoid, which is posterior in position, and nearer to the mesial line. This interpretation is founded upon Mr. Hulke's reading of the Lacertilian coracoid; but is unsupported by evidence, because the structures compared are morphologically different, and could only be brought into comparison, I submit, by first removing the precoracoid from the Lacertilian shoulder girdle, when the notch or foramen in the coracoid of the Lizard would face towards the scapula, as in *Nothosaurus*, with a similar open angle between the two bones. So far from the relations of what I regard as the cartilaginous precoracoid of *Nothosaurus* to the scapula and coracoid being different from what they are in *Ichthyosaurus*, they seem to me to be as nearly identical as possible in a widely divergent order of animals. For, in my conception, there is no reason why the notches which Mr. Hulke regards as representing the coracoid foramina should not entirely disappear under ossification of the anterior margins of the coracoid bones, so as to bring what are at present the two widely separated anterior processes of the coracoids into close union with each other, when the difference from *Ichthyosaurus* would be less apparent. As my meaning has not been clearly understood, I offer a restoration of the shoulder girdle of *Nothosaurus mirabilis*, showing what I conceive to be the position of the cartilaginous precoracoid.

This identification of the precoracoid foramen does not depend upon the evidence from *Nothosaurus* only. There are small unnamed Nothosaurs, figured by von Meyer in his 'Saurier des Muschelkalks,' Pl. XXXIII, fig. 45, &c., showing on the inner side of the scapula a notch with ossified margin (fig. 7, *f*), altogether distinct from the cartilaginous margin of the bone behind and in front of it, and therefore there is no doubt that both scapula and coracoid in those animals contributed to the formation of a foramen between those bones, which was completed by cartilage, as in the Ophthalmosaurs already referred to. The argument concerning that cartilage is in every respect the same as that offered in *Ichthyosaurus*. There is, however, this difference. The animal is fundamentally different in general organisation. Nothosaurs were for a long time included with the

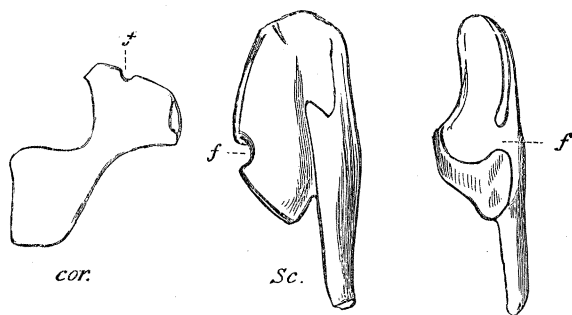


FIG. 7.—*cor.*, right coracoid ; *Sc.*, right scapula, visceral and internal aspects ; *f*, portion of the scapulo-coracoid foramen. (After von Meyer.)

Sauropterygia; but since 1882 it has been clear to me that they form a different order, which is intermediate between the Sauropterygia and the Anomodontia. And although it may not be possible at present to fully establish this conclusion, it is one in support of which evidence can be adduced. It is on this account that the interpretation of the shoulder girdle in *Nothosaurus* has appeared to me to have a two-fold significance as establishing, first, by comparison with *Plesiosaurus*, the true nature of the clavicles of Sauropterygia, and secondly, by comparison with the Anomodontia, I think it places beyond question the true nature of the precoracoid. The large questions of organic affinity I regard as safe bases for the morphological interpretation of the skeleton. If I do not enter into discussion of *Lariosaurus*, it is because the scapulæ are displaced, and I have already referred to the type on a former occasion.

The Anomodont comparison is important. First there is a notch in the Anomodont scapula which I regard as a Mammalian character, and this notch is completed externally by the ossified precoracoid, and passes obliquely through that bone, so as to excavate the coracoid. The relations of these bones are shown in *Pariasaurus Baini* (fig. 2), and in many South African Anomodonts. As the specimens have been figured, it may be sufficient to refer to the figures as showing that the relations of the precoracoid to the coracoid and scapula are almost identical with those which I have suggested for the cartilaginous precoracoid in *Nothosaurus* (fig. 6) and *Ichthyosaurus* (figs. 1 and 4). Mr. Hulke has not pointed out any difference in this part of the skeleton from the Ichthyosaurian or Nothosaurian type, which would invalidate my interpretation that the difference between them, which is most essential in plan, is that Anomodonts have the precoracoid ossified. The ossification occupies substantially the same position which I have attributed to the precoracoid in the types in which it is supposed to

be cartilaginous. The weight of this comparison consists first in the direct resemblance of plan between the Anomodontia and Ichthyosauria in the clavicular arch and the shoulder girdle, where the difference is essentially that in the former the precoracoid is ossified, while in the latter there is a vacuity in the position which the precoracoid occupies in the former. And secondly, although the resemblance in detail in this region between the Anomodontia and the Nothosauria is less close, as shown in the construction of the scapula, there is a closer organic affinity between these types, which gives importance to the resemblances which have been stated.

The anatomical comparisons which have been made amount, I submit, to as close an approximation to proof that the precoracoid was represented by cartilage in *Ichthyosaurus* as could be given of a structure which is necessarily not preserved in the skeletons in which it has been argued to have existed. They may be thought to justify the suggestion of a cartilaginous precoracoid in *Ichthyosaurus* which was advanced in my paper.

#### *The Sauropterygia.*

I have regarded the Sauropterygian shoulder girdle as comprising the same bones as the shoulder girdle in Ichthyosauria and Nothosauria, and urge that the difference between them is that there is no trace of a precoracoid in Plesiosaurs, even the cartilage in the shoulder girdle indicated in those orders having disappeared. The clavicular arch in all three orders appears to me to be formed of the same elements, which I regard as being typically an interclavicle and two clavicles. These identifications are contested by Mr. Hulke, who advances the hypothesis that the bone which I regard as a scapula is a precoracoid in its inner portion and a scapula in its outer portion; and secondly, the hypothesis that the bones which I regard as a clavicular arch are not homologous with clavicular bones, but are a new kind of arch, formed from omosternal bones. Both of these hypotheses seem to me untenable, for the reasons presently to be stated. In the first place, attention may be directed to the precoracoid. Mr. Hulke has not explained why it is morphologically necessary to find a precoracoid in Sauropterygia when its existence is not affirmed by him in Ichthyosauria. He would apparently admit (fig. 4, *loc. cit.*, p. 241) that in Lacertilia the precoracoid loses its individuality by union with the coracoid, and, as I have stated, there are many examples which probably show such a condition among extinct animals. But here is a suggestion to blend the precoracoid with the scapula, to which no parallel can be found, as I believe, in true Reptiles, recent or fossil. It is not suggested by Mr. Hulke that any specimen exists in which there is a trace of a division of the

anterior bone of the Plesiosaurian shoulder girdle in the way which he represents by shading in his figure (fig. 8, p. 246) of the crushed and imperfect Woodwardian specimen, which may be compared with the figure given by myself in 1865 from a photograph, in the 'Annals and Magazine Nat. Hist.,' series 3, vol. 16, Pl. XV. In that specimen there is a partial longitudinal division, which I believe may be better explained by fracture. When the specimen was originally described, Plesiosaurian clavicles had not been identified, and I thought the division might represent a clavicle external to the scapula, and, although that view became untenable with the discovery of the clavicles in 1874 ('Quart. Jour. Geol. Soc.,' vol. 30, p. 444), I have since suggested that the ossification, if it ever were distinct, may represent the epiclavicle (*ec*, fig. 2) which extends along the superior margin of the scapula in *Pareiasaurus Baini*. It must be remembered that in *Plesiosaurus* this supra-arthroïdal process of the bone is very thin, and ascends nearly vertically, so that it would be peculiarly liable to fracture. The specimen is elucidated by no other example in the separation and displaced position of the ascending process of the scapula; and, since it differs from other specimens from the Lias only in the horizontal and displaced position of that process, I have no doubt the specimen is delusive, in so far as it appears to suggest two separate bones. If the bones had been separate there would have been presumably a cartilaginous division line between the two elements, if both entered into the formation of the humeral articulation, in the position in which a division is figured by Mr. Hulke, whereas there is no such indication of division in the specimen, or in any other specimen.

This crushed bone is insufficient to support and sustain a new reading of the homologies of the great bones of the Sauropterygian shoulder girdle. If there is no other objective evidence in the Plesiosaurian skeleton, and Mr. Hulke mentions no other, there is, I submit, no evidence in support of a precoracoid in the Sauropterygia, except such as may result from comparison of Plesiosaurian bones with those of other animals, since the division drawn ('Roy. Soc. Proc.,' vol. 52, p. 246) is not in the line of fracture.

I am in entire agreement with Mr. Hulke in comparing the shoulder girdle of Sauropterygia with that of Chelonia, these orders being grouped in the Sauromorpha, in the scheme of classification given in 1891 ('Roy. Soc. Proc.,' vol. 49, p. 520). The difference between the views of Mr. Hulke and myself consists in the method of comparison and its results. In Sauropterygia the bone in advance of the coracoid which joins it by suture is in the same plane with the coracoid. In the Chelonia the bone which has the same relation to the coracoid is nearly vertical to the coracoid, or only inclined slightly forward. The Chelonian bone consists of two slender rays,

which diverge so as to include between them a large angle. The ventral ray extends transversely inward to the median ventral line towards its fellow, in a way to which no part of the bone in the genus *Plesiosaurus* offers a parallel; the dorsal ray ascends to the carapace in a way which is equally unparalleled in *Plesiosaurus*. There are two methods in which these structures may be compared in the two groups.

First, we may suppose, as Mr. Hulke does, that although the coracoids have no median union with each other in Chelonians, they are strictly comparable with the Plesiosaurian coracoids, which unite by a median suture. Then the ray of the anterior bone, instead of extending inward to meet its fellow, as in Chelonians, may be supposed to be directed forward to become an expanded plate, uniting with its fellow in some genera of Sauropterygia (e.g., *Muraenosaurus*) in the median line, and in such cases it may send a ray back to make a median union with the coracoid. Further, the vertical or forwardly inclined bar of the Chelonian bone is supposed in Plesiosaurs to be represented by the compressed plate which, ascending from the horizontal ray, extends above the articular surface for the humerus. Hence the two rays of the bone in Plesiosaurs are in two planes, one horizontal, and the other vertical, while in Chelonians the two rays may be regarded as substantially in the same plane, which, in so far as it is not vertical, is inclined forward. In both groups of animals Mr. Hulke names the ventral ray precoracoid, and the dorsal ray scapula.

There is another way of bringing the two types of shoulder girdle into comparison. If the elongation of the neck in *Plesiosaurus* is supposed to be brought about by an augmentation in number of the vertebræ from a type in which they were less numerous, then there is some ground for anticipating that the scapula, if originally in such a vertical position as it holds in Chelonians, would have its free superior end carried forward, until it might come to be in the same horizontal plane with the coracoid.\* This is what I infer to have happened, and to represent the mutual relations of the parts, so that the forwardly directed horizontal plate of bone in *Plesiosaurus* would be homologous with the vertically directed bar of bone in Chelonians which all anatomists agree in naming scapula. And, therefore, there would be nothing in the Plesiosaurian shoulder girdle to correspond to the ray of bone which is directed inward ventrally in Chelonians, and that element, I suppose, to have practically disappeared from the Plesiosaurian skeleton. Hence the ascending ray of the scapula in *Plesiosaurus*, which extends above the humeral articulation, would not be homologous with the vertical ray of the scapula

\* Some generic modifications of the Plesiosaurian pectoral arch, 'Quart. Jour. Geol. Soc.,' vol. 30, 1874, p. 439.

in Chelonians. There is in this interpretation an element of simplicity, because the scapula is simply inclined forward in a way to which there may be some slight approximation in Chelonians, which brings the two types of shoulder girdle into easy comparison. The coracoids in Plesiosaurs meet each other in the median line, and this condition has, I suppose, led to the atrophy and non-development of such a ray as Mr. Hulke terms the precoracoid, but which I believe to be a portion of the scapula,\* on the hypothesis that such a ray may have once existed.

The choice between these methods of interpretation may depend upon the name adopted for the bone which most anatomists have termed scapulo-precoracoid in Chelonians, for if there is a precoracoid in the Chelonian, which is blended with the scapula, so as to be inseparable from it, then there would be some ground for Mr. Hulke's contention that the precoracoid was represented in the scapula of Plesiosaurs, even though there would be a difference of opinion still as to the position in which it was to be sought for, which would depend upon views as to the way in which the Plesiosaurian girdle was formed. Professor W. K. Parker termed the inner ray of the Chelonian bone precoracoid, and appears to base his interpretation chiefly upon the condition of the bones in the African Ostrich. It is stated ('Ray Soc.,' "Shoulder Girdle," p. 141) by the late Professor W. K. Parker, of *Chelone Mydas*, "There is nothing that can be called 'præ-' or 'meso-scapula,' save the swollen part in front, which passes uninterruptedly into the precoracoid; this front fork forms, with the scapula, a gentle arc (Pl. XII, fig. 3); it is of the same thickness, nearly of the same length, and has no separate osseous centre, the two bars being hardened by one ectosteal sheath." I gather that Professor Parker's observations were all made upon the ripe embryo or newly hatched young. A somewhat younger specimen in the Museum of the Royal College of Surgeons has by the kindness of Professor Stewart been examined for me by Mr. R. H. Burne, but without showing any indication of composite structure. Mr. Hulke quotes H. Rathke's account of the earlier ossification of this bone, in which it was found that each of the two limbs of cartilage has a distinct sheath, and that they had not quite reached each other at the stage described, in some types; while in another type the two limbs were united by ossification on their inner side. I can find no evidence in this condition that the bone which is termed precoracoid is distinct from the bone which is termed scapula, nor can I find in Rathke's account of the Chelonian shoulder girdle any evidence that he supposed that the two rays were distinct from each other, and that each contributed to the formation of the hollow of the shoulder joint. What Rathke describes is in complete harmony with the structure of every

\* This view has also been adopted by Professor George Baur.

Chelonian bone, recent or fossil, which I have examined, so far as can be judged from the ossified bone, and it is closely comparable to the conditions of ossification of Plesiosaurs on the one hand, and of Amphibians on the other, in which the original cartilage of the humerus and femur becomes sheathed by an external layer of bone, leaving the cartilage in the position of an epiphysis, which penetrates more or less conically from the articular joint of the bone into the sheath, becoming an ossification which sometimes blends with it, and is sometimes for a time separate in the young state.

There is no evidence advanced that two distinct cartilages enter into the composition of the part of the glenoid fossa formed by this bone, and I affirm that its two rays are sheathed separately, because, owing to the original form of the cartilage, it would not be conceivable that the sheaths should be formed in any other way. But in his account of the young *Sphargis*, Rathke expressly states that the two sheaths coalesce when they meet each other, and therefore form one sheath, without any indication of a primitive separation between the two rays of ossification which afterwards became obliterated. Just as the ossification of the humerus of a Plesiosaur in three portions does not make that bone any the less a humerus, so the ossification of the scapula in a Chelonian in two or three parts, of which the articular part was originally cartilaginous and two are the coalesced ectosteal sheaths, does not seem to me to make that bone any the less a scapula in Chelonians. There is therefore no proof that the bone in Chelonians is anything but a scapula, or that the precoracoid is present in the Chelonian skeleton, any more than in the Plesiosaurian skeleton.

It only remains to point out that the ascending process of the Plesiosaurian scapula is homologous with that which is developed backward in the Nothosaurian scapula (figs. 6 and 7), and I have no doubt that both are homologous with the blade of the scapula in Ichthyosaurs and Anomodonts. But, in proportion as this scapular blade is developed, so does the scapula acquire a position which is posterior to the coracoid; while that position is the result of a special development of a new structure which ascends in these animals external to the ribs, above the humeral articulation. Its development is accompanied in Anomodonts by an atrophy of all that part of the scapula which had originally extended in advance of the articulation. This view may be hereafter established by further evidence. If the older view, which Mr. Hulke puts forward, should be preferred, there would still remain the evidence that the precoracoid has no existence in Chelonia, and therefore inferentially has no existence in Sauropterygia. So that the bone which extends in Plesiosaurs anterior to the coracoid would still be the scapula, and the shading which Mr. Hulke places upon it, dividing it into precoracoid and scapula, would be a delusive indica-



tion of an osteological separation of one bone into two bones which has no existence.

But the effect of the extraordinary difference in number of vertebrae in the several regions of the body in Plesiosaurs and Chelonians cannot, I think, be ignored in judging between the hypothesis of morphological displacement of one limb of the scapula as against morphological development of the other limb, when the bone is considered in Plesiosaurs from the point of view of a Chelonian comparison. The morphological resemblance with Chelonians is not so close as to solve the problem by comparison only.

Finally, there remains the clavicular arch, or, as Mr. Hulke terms the bones, omosternalia. Mr. Hulke regards the interclavicle as derived from the mesial ends of the clavicles (p. 246), and the omosternum as derived from the epicoracoids, so that in existing animals these structures appear to originate differently. Unfortunately there are no epicoracoids preserved in the Sauropterygia, so that it is impossible to base the nomenclature which Mr. Hulke prefers upon a morphological or structural basis.

The reason why the omosternal interpretation has been preferred by Mr. Hulke is stated (p. 252) to be the undisputed deep position of the bones, which are sometimes completely hidden by the scapulæ, and which always rest upon the visceral, as distinguished from the ventral, surface of those bones; and this, coupled with the composite structure, is the only reason advanced. I would compare this nomenclature for the bones, which I have figured as clavicular ('Roy. Soc. Proc.' vol. 51, pp. 129, 131, 133, 140, 147, &c.), with the nomenclature adopted by Mr. Hulke for the corresponding bones in *Nothosaurus* ('Proc. Roy. Soc.', vol. 52, p. 240). The interclavicle and clavicles are there represented, and the clavicles are correctly shown to extend on the deep-seated or visceral surface of what I regard as the scapulæ, precisely as in the Sauropterygia. So that the supposed proof from deep-seated position, which shows the bone not to be clavicle but omosternum in *Plesiosaurus* is exactly the same as that which is considered by Mr. Hulke to prove the bones which correspond to them in position in *Nothosaurus*, to be not omosternal, but clavicular. In both types the scapula is placed horizontally in advance of the coracoid, although there are some differences of form in the bones as compared with the Plesiosaurian genera. But all von Meyer's specimens show that the clavicles in *Nothosaurus* extend upon the visceral surfaces of the scapulæ, precisely as in *Plesiosaurus*. Mr. Hulke does not question that the bone named scapula in that genus represents the scapula. There is no suggestion that it includes the precoracoid; and it appears to be suggested that the part of the coracoid which is internal to the notch in the anterior part of that bone is precoracoid; so that the precoracoid would be an indivisible

portion of the coracoid. Hence, apparently, the difference in interpretation, the omosternum being assumed to join the precoracoid when it is present, while the clavicle is assumed to join the scapula. This interpretation is entirely hypothetical; for there is no more evidence in favour of the Nothosaurian coracoid being a coraco-precoracoid than there is in favour of the Plesiosaurian scapula being a precoraco-scapula. And therefore there is no foundation for the difference of interpretation which would name the bone which rests upon the visceral surface of the anterior element of the shoulder girdle in *Nothosaurus* a clavicle, and that which rests upon the visceral surface of the bone which occupies the same position in *Plesiosaurus* an omosternal bone. This arch in *Nothosaurus* consists of a small median piece and two long lateral pieces, which may, I think, be compared with the elements figured in *Plesiosaurus* ('Roy. Soc. Proc.,' vol. 51, p. 129), although the median element is much larger in the Plesiosaur, and the lateral elements are much shorter. Until some evidence is forthcoming to show that the bones which form an arch in the same position and are similarly situate on the visceral surface of the bones of the shoulder girdle are different, there is no justification for applying different names to them, or assuming that they are not homologous. In some of the smaller Nothosaurs figured by von Meyer it is evident that the anterior visceral surface of the scapula was smooth, so that the clavicle joined the scapula by squamose overlap, and not by suture, as in the genus *Nothosaurus*, thus approximating more nearly to the condition in *Plesiosaurus*.

The circumstance that the interclavicle in *Nothosaurus* and its allies is not wedged in behind the visceral surface of the coracoids, is necessarily a consequence of the small antero-posterior development of the median union between the coracoid bones, and the great length of the clavicles, by which the interclavicle is carried forward in the middle of an arch which is convex in front; while in Plesiosaurs what I believe to be the homologous arch is shorter and similarly directed backward. But there is no difference in plan. In Plesiosaurs (*loc. cit.*, p. 129) the clavicles are directed backward exactly as in *Nothosaurus*, and it is only the anterior margin of the interclavicle which is concave in front. There is so much in common in the structure of the skull, in the vertebral column, in the pelvic arch, the shoulder girdle, and limbs between the Sauropterygia and Nothosauria that there are probably no two other well differentiated orders of animals which have greater organic affinity with each other, and, therefore, although I have proposed to recognise a cartilaginous precoracoid in *Nothosaurus* of which no evidence is available in *Plesiosaurus*, I can see no ground for supposing that the bones of the shoulder girdle which are actually preserved are not severally the same as in the Sauropterygia.

There is another point in Mr. Hulke's argument. He adopts the classification of the shoulder girdle bones into primary or cartilaginous and secondary or membranous. There is no doubt that in the immature *Plesiosaurus*, in which all the indubitable cartilage bones show unossified cartilaginous surfaces and margins, the two bones figured ('Roy. Soc. Proc.', vol. 51, p. 133) which I regard as clavicles are completely ossified, with sharp well-defined margins, and show no signs of immaturity; and I therefore regarded them as membrane bones. Some of the clavicular bones figured at the same time (*loc. cit.*, p. 131) are almost as thin as bones could be, and in marked contrast to the cartilage bones of the skeletons with which they are severally associated, although there are other examples in the collection of Mr. A. N. Leeds, of which he has since had the kindness to send me drawings, which are considerably thicker. If these bones had been omosternal bones, segmented from epicoracoids which are cartilages, presumably they would have been cartilage bones. But the immature specimens to which I have referred show no indication of having had a cartilaginous origin. Mr. Hulke states that it is possible that the bones which he terms omosternal are membrane bones, but adds that this is not yet absolutely certain, and yet, having urged that the distinction between the two groups of bones rests upon their different origin in the embryo, concludes that the weight of evidence is still in favour of an omosternal homology.

I am unable to imagine any evidence more conclusive than that which has been brought forward, based upon the condition of the bones themselves in the young *Plesiosaur*, and comparison with the condition in *Nothosaurus*.

From 1874 ('Quart. Jour. Geol. Soc.'), I have indicated affinities between Sauropterygia and other animals. The comparisons which have weight are indicative of a common plan between the animal types compared. Affinities which can thus be demonstrated may justify views of homology in interpreting obscure parts of the skeleton, which are more valuable than the views based upon resemblances of form found in isolated bones in animals which are widely different in organisation. I have formerly pointed out elements of the skeleton in which *Plesiosaurs* show characteristics of *Amphibians*, as in the mode of ossification of their long bones. Exactly the same condition of ossification is found in *Nothosaurus*. If this is an *Amphibian* inheritance which amounts to identity of plan in the construction of the limb bones, in a way which marks these two orders of animals off from other groups, it does not furnish an *a priori* ground for assuming that the coracoid, the scapula, and the arch of bones in front of these are all morphologically different in the *Plesiosaurs* and *Nothosaurs*, but rather that they are substantially the same.

If the significance of these Amphibian characters is further found, as I urge, in a sequence of affinity between the Sauropterygia, Nothosauria, and Anomodontia, we should be justified in anticipating that there might be a community of plan in the shoulder girdle of those groups which would enable homologous elements to be recognised. Until such comparisons fail, they cannot be disregarded.

The view which I have discussed in justification of that offered to the Royal Society in 1892 may be summarised in the statement that the Anomodont is a type in which the precoracoid is ossified; that in the Nothosaur the precoracoid has ceased to be ossified, but is represented by cartilage; while in the Plesiosaur the precoracoid cartilage appears to be lost. But with this change there is no change of plan in the clavicular arch, other than results from the different habits of the several orders of animals and the forms of the girdle bones with which the arch is associated.

XIII. "Researches on the Structure, Organisation, and Classification of the Fossil Reptilia. Part VIII. On further Evidences of *Deuterosaurus* and *Rhopalodon* from the Permian Rocks of Russia." By H. G. SEELEY, F.R.S. Received June 10, 1893.

(Abstract.)

The author endeavours to separate the Labyrinthodont remains, distinguished by having teeth ankylosed to the jaw, from such as belong to animals having a Theriodont type of dentition. The genera founded upon cranial fragments which show the Theriodont type are *Deuterosaurus*, *Rhopalodon*, and *Dinosaurius*. The skull in *Deuterosaurus* is described from new materials, which make known the structure of the palate and other cranial structures. The palate is of Plesiosaurian type. The back of the skull is a vertical plate, and the brain cavity rises in a long vertical tubular mass to the parietal foramen. The quadrate bones descend below the foramen magnum in a way that is best compared with Plesiosaurs.

The articular end of the lower jaw is identified among bones figured by von Meyer.

The skull of *Rhopalodon* is nearly complete, and has a general resemblance to the skull of the South African Dicynodont *Ptychognathus*. The orbit is defended with a sclerotic circle of bones. Whereas in *Deuterosaurus* there is only one molar tooth, in *Rhopalodon* there are apparently eight molar teeth, which have the posterior edge finely serrated.

The vertebræ are known from isolated and connected specimens which indicate a larger number than usual of rib-bearing presacral

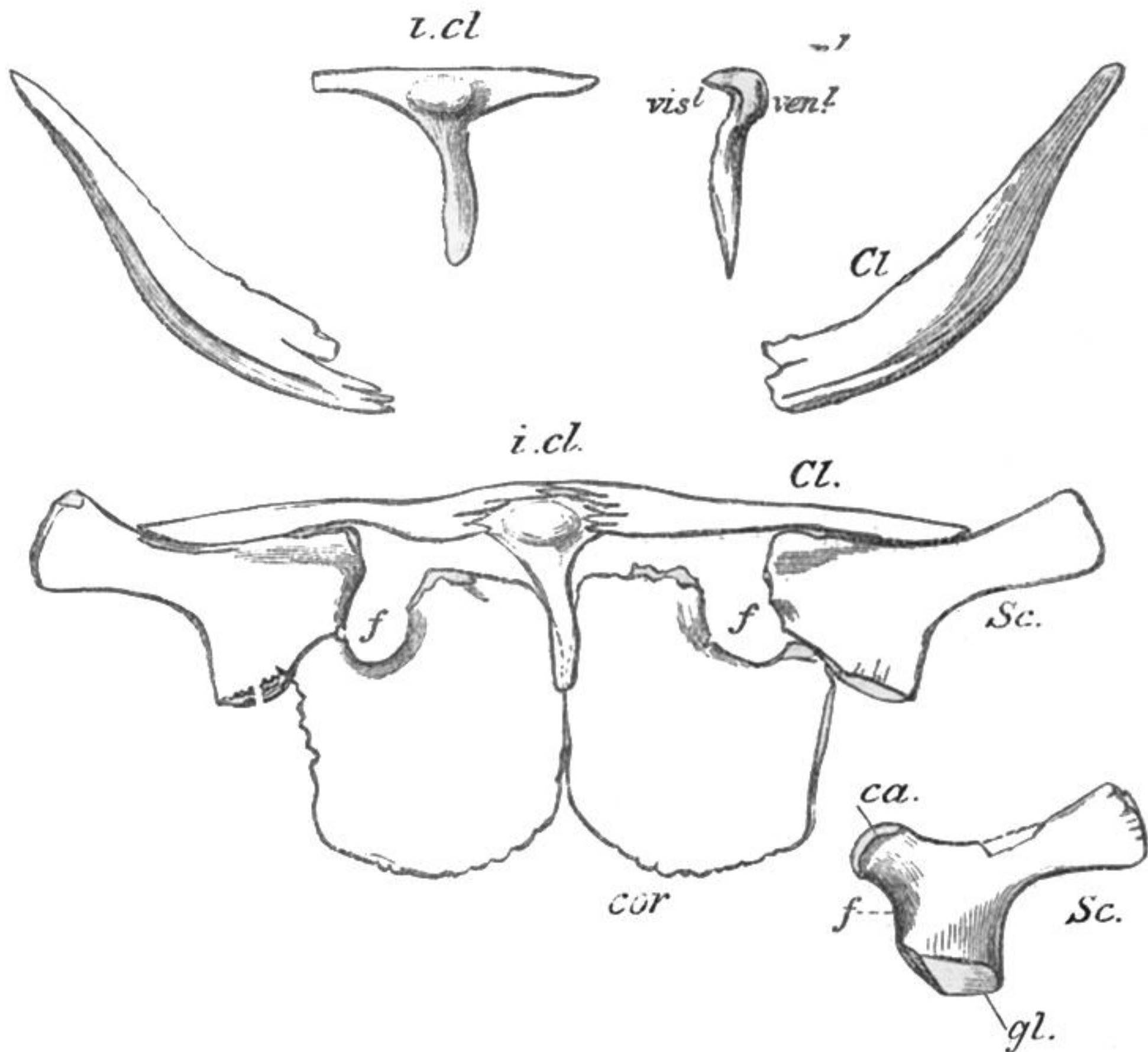


FIG. 1.—Shoulder girdle of *Ophthalmosaurus*. *i.cl.*, front aspect of interclavicle; on the right is a side view of this bone, showing its ventral and visceral contours. Beneath it are the posterior surfaces of the right and left clavicles (*Cl.*). Below this all the bones of the shoulder girdle are put together. The interclavicle is embraced by the clavicles; and (*cor.*) coracoid and scapula (*Sc.*) contribute to enclose the coracoid foramen (*f*). On the right and lower corner is an isolated scapula, with the margin of the coracoid foramen (*f*) completely ossified, preserving the cartilaginous surface (*ca.*). *gl.*, humeral articulation.

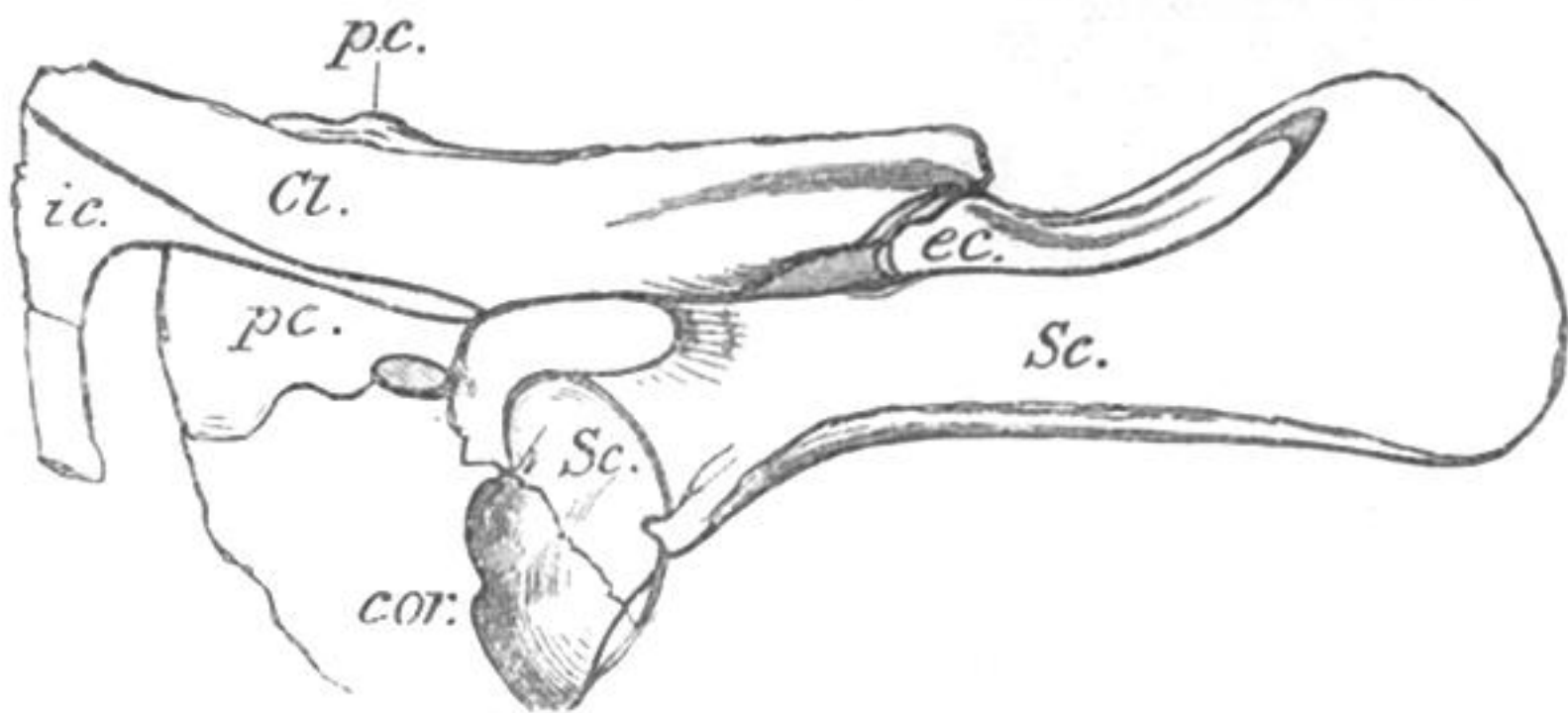


FIG. 2.—Left shoulder girdle of *Pareiasaurus Baini* as the bones were found before the matrix had been removed to separate the clavicular arch from the scapular arch. *ic.*, interclavicle; *Cl.*, clavicle; *pc.*, precoracoid; *cor.*, coracoid; *Sc.*, scapula; *ec.*, epiclavicle.

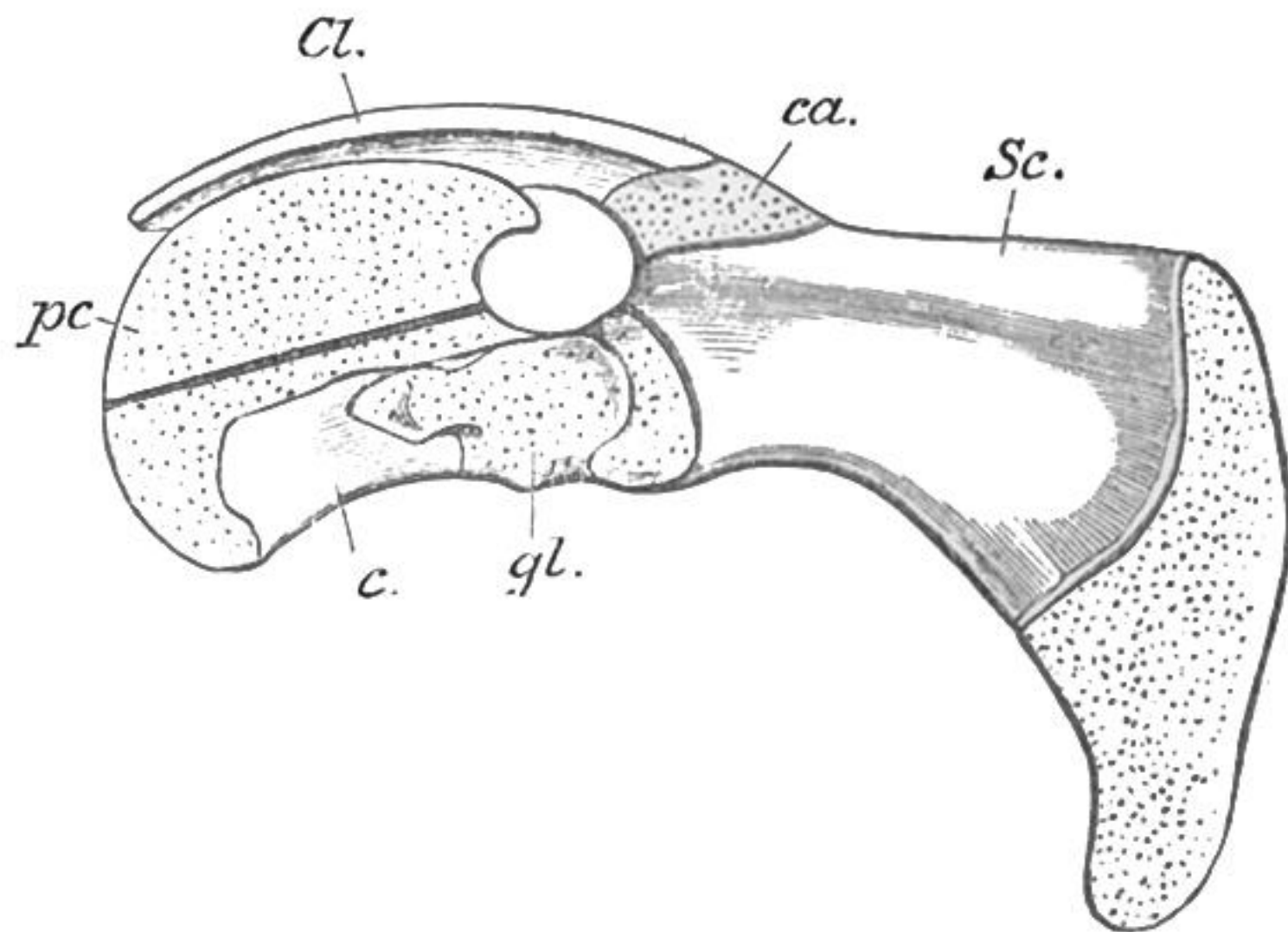


FIG. 3.—Shoulder girdle of a young *Ornithorhyncus*, after G. B. Howes, reduced and reversed. The dotted parts (*Ca.*) are cartilage; *Cl.*, clavicle; *pc*, precoracoid; *c*, coracoid; *Sc.*, scapula; *gl.*, humeral articulation.